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BREEDING METHODS AND INHERITANCE IN THE GREENHOUSE CARNATION

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University of Alberta

April, 1946

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The undersigned hereby certify that they have read and recommend to the Committee on Graduate Studies for acceptance, a thesis on "Breeding Methods and Inheritance in the Greenhouse Carnation", submitted by Alexander C. Patterson, B.Sc. in partial fulfilment of the requirements for the degree of Master of Science.

Professor

Professor

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BREEDING METHODS AND INHERITANCE
IN THE
GREENHOUSE CARNATION

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A THESIS

submitted to the University of Alberta
to fulfil approximately one-half of the
requirements for the degree of
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INTRODUCTION

Carnations are the second largest greenhouse crop in Canada and the United States, being exceeded only by roses(10). Although rose growing has a greater commercial value, it requires a higher capital investment, more careful treatment and culture and is thus confined to the larger florist establishments. The carnation, on the other hand, because its culture is relatively easy - it requires only a cool house and is easily propagated - appeals to the small grower. Undoubtedly there are more growers directly interested in carnation culture than in any other greenhouse crop. Despite the widespread popularity of the carnation, knowledge of breeding methods and inheritance of many characteristics has been limited.

The object of the present project is to study the inheritance of some of the characters of the carnation, to study breeding methods, and to develop better varieties than those presently available to the grower.

In the literature review, and in the account of the work done so far, mention will be made of a number of problems which so far have not been studied, but which deserve attention, and can form the basis for further work.

HISTORY

The name of the genus Dianthus was evidently adopted by Linnaeus from the work of the Greek writer Theophrastus (about 300 B.C.) who named a small, single, native Pink, "Dianthus" (dios - divine, anthos - flower). A translation[6] of Theophrastus' "History of Plants" says "The Greeks cultivated roses, pinks, violets, narcissi, and irises". The specific name caryophyllus (Greek caryon- nut, phyllon - leaf) has been applied to the clove tree (Caryophyllus aromaticus); because of the clove-like fragrance of the carnation this name was applied to it.

The cultivation and development of the earlier forms is difficult to trace. Allwood[1] claims that William the Conqueror brought its wild ancestor to England from Normandy.

In the 16th Century the Border carnation, a variety of D. caryophyllus, was grown in England and is still widely cultivated. It is a half-hardy, herbaceous perennial, having a definite rest period each year. It has a smaller blossom and a shorter, bushier form than the greenhouse carnation.

It was known in the 16th Century according to Murray[29] as "gillofre", "gillyflower", "coronation", "cornation", and "carnation". "Gillofre" is from the Old French clou de girofle - the name of the spice clove. The English "clowe-gilofre" was commonly shortened to "clowe", for the spice, the

full name adhering to a flower, the clove-pink. Finally with the corruption of "gilofre" to "gillyflower", the latter name without the "clove-", has passed on to various scented flowers having no connection either with the spice or with the clove-pink. Lytes "Dodoens, a Niewe Herball, or Historie of Plantes" (translated in 1578 by H. Lytes from Rembert Dodoens) is quoted at length by Murray: "The cloue gillofer: the flowers grow....out of long round smooth huskes and dented or toothed above like the spice called cloaues....do all smell almost like cloaues....The pynkes, and small feathered Gillofers, are like to the double or cloaue Gillofers in leaues, stalkes, and floures, sauing they be single and a great deale smaller....In English gardens Gillofers, Cloaue gillofers, and greatest and brauest sorte of them are called Coronations or Cornations". Murray says, "Some 16th Century writers give one form of the name as "coronation" apparently from its 16th Century specific name <u>Betonica coronaria</u>" and it is generally agreed that this is the original form. It became corrupted to "carnation", probably because of the preponderance of flesh-pink colored flowers. Evelyn[22] in 1695, mentions the plant at 14 different places in his book and each time as "carnation". This spelling has been retained ever since.

The development of a variety that would bloom continuously is attributed by Baur[6] to a French gardener, M. Dalmais,

who in 1840 crossed a Border carnation with a Flemish carnation which is also a variety of D. caryophyllus. However Allwood[1] claims that the greenhouse carnation is a hybrid of the Border carnation and the Indian Pink (D. chinensis). Although he is alone in this belief his opinion cannot be lightly disregarded as he has probably done more work with, and hybridization within, the genus than has anyone else and therefore should be more familiar with the various species and their behavior. At any rate in 1856 an American commercial firm imported some of these plants from France and used them for breeding their own varieties. Since then the industry has grown rapidly and many improvements have been made in color, form, and growth habit. Over 1200 varieties have been introduced in America. The English have also developed the carnation to a certain extent. They call it the "perpetual", "tree", or "Malmaison" carnation. In America, the word "greenhouse" has become the standard adjective.

The American Carnation Society was organized in 1891 and has done much to popularize the flower and to encourage carnation growing. In the late 1920's and early 1930's, the improvements in the American types had become so marked that English and European growers imported American varieties to improve their own stock.

LITERATURE REVIEW

Propagation

There are three methods of propagating carnations[6], namely by seed, layering, and cuttings. Owing to the heterozygous nature of the plant, seed does not follow true and varieties cannot be perpetuated in this manner. Layering, which was used 30-50 years ago[12] is a laborious and not a very productive method. Cuttings are now used exclusively as the means of propagation. The larger growers have specialized to such an extent that they have propagating houses which are devoted solely to rooting the cuttings.

There are two types of cuttings, namely 'heel', and 'top' or 'piping'. The heel cuttings are taken from short lateral branches growing from the leaf axils; these have more woody tissue at the base and shorter internodes than have top cuttings. Top cuttings are selected from elongated vegetative branches; the internodes are about an inch or more in length. Carter[12] like most commercial growers prefers heel cuttings. Laurie and Chadwick[26] state that if a cutting is vigorous and healthy, the type used is immaterial. Decker and Weinard[19] carried out an experiment with several varieties which were grown in different fertilizer plots. They took top and heel cuttings, slitting the base of some to a depth of about $\frac{1}{4}$ inch. They found that the cuttings rooted best if they were taken from plants grown in an excess of potassium, but that

varieties reacted differently to the other variables. Some rooted better from heel cuttings and others from top cuttings; some rooted better from slit cuttings, and others from unslit cuttings. Significant differences were not obtained in the number and quality of flowers produced from top, heel, slit or unslit cuttings. They concluded that varieties differ as to the maturity of the wood from which they root most freely, and that, in general, varieties that are difficult to root improve their strike when the cutting is slit at the base.

Seed Production

From the literature it appears that all the workers have carried out the actual breeding during the winter months in the greenhouse.

Stuart[38] notes a difference in the quantity and quality of seed produced at various times during the commercial growing season. He concludes that crosses made in the early part of the season (November and December) give (a) a higher percentage of successful crosses, (b) a much larger number of seeds per capsule, and (c) a higher percentage of germination, than do crosses made in January or February. He attributes this to the greater vigor of the plants at this time. Hall[23] who had previously noted a similar tendency, attributes it more to seasonal influence.

Harris[24], in applying statistical analysis to Stuart's[38] figures, finds a relatively higher failure to germinate among

the seeds which are produced many in a capsule. This contradicts Stuart's statement that there is a higher percentage germination among seeds set early in the year. However, Harris does not attach any significance to his results because of the low population.

Dorner[20] considers that December, January and February are the best times to cross, as it is then that the plants show their best development and therefore the best time to select parents.

Stuart[38] points out that there is a wide variation in the number of seed produced between different varieties. He recommends that prolific seed parents, when their progeny have proved satisfactory, should be propagated for the express purpose of breeding.

Inheritance in the Carnation

Inheritance of Color

No scientific approach to the inheritance of color was attempted until 1939. Before that time Dorner[20] and Baur[6] simply recommended that more satisfactory results would be obtained by confining the breeding to like colors, i.e. white x white, pink x pink, etc. However, in 1939, Mehlquist[27] made a very comprehensive study of inheritance of color in the "self" colors*. He identifies 6 independent factors, and calls them _Y_, _I_, _A_, _S_, _R_, _M_. He summarized their actions as

*He is in the process of preparing a paper on the inheritance in the "variegated" colors.

follows: "Y controls the production of yellow anthocyanin, I controls the production of ivory anthocyanin. It is epistatic to Y. A is the basic anthocyanin factor. It is normally effective only in the presence of both Y and I. Partial anthocyanin is possible in the absence of I, the resultant color varying from salmon-yellow to maroon, depending on what specific anthocyanin factors are present. S controls the production of scarlet-red anthocyanin, its recessive allele s dilute red or salmon. R controls the production of crimson-red anthocyanin, its recessive allele r permits the production of scarlet-red anthocyanin only. M modifies the colors of the red series to the corresponding colors of the magenta series. It has no effect in the acyanic group and probably little effect in the transition group".

Inheritance of Abnormal Types

The high percentage of abnormal types, which result from crossing and selfing has been observed by a number of workers[5,17,21,38].

Mehlquist[28], in 1941, studied the inheritance of nine of these types. Each type differs from the normal in a single recessive factor. The factors are: alb - albino seedling, lethal; yel - yellow seedling, lethal; lut - lutescent seedling, lethal; cb - club-neck, nearly always lethal; vir - virescent, a chlorophyl deficient type, semi-lethal; dw - dwarf, extremely short plant, less viable than

the normal type, highly sterile; sto - stocky, short, stocky plant, somewhat less viable than the normal type, highly sterile; and th - thin, an annual type, less hardy than the normal type, but fully as fertile. He says "due to the prevalence of these abnormal types, most of which can be traced directly to well known commercial varieties, or their immediate derivatives, it would seem highly desirable to have on hand for breeding purposes, strains which are free from factors causing undesirable types and at the same time possess commercially desirable color."

Inheritance of Disease Resistance

There are a number of diseases that attack the carnation. The most common are carnation rust and stem rot.

(a) Carnation rust (*Uromyces caryophyllinus* (Schrank) Wint.)

The symptoms are expressed by characteristic yellowish-brown pustules of rust on the leaves and stems. A heavy infection will weaken the plants to such an extent that the crop becomes unprofitable. Further, the appearance of infected leaves or stems lowers the market price of the cut flower.

Dorner[20] and Batchelor[5] state that resistance to rust is highly desirable in new varieties, and Baur[6] and Laurie and Chadwick[26] recognize that varieties vary greatly in their susceptibility to rust. However, no work has been done to determine the inheritance of rust resistance.

(b) Stem Rot (Corticum vagum (B & C) Rhizoctonia solani (Kuhn))

This disease is very prevalent whereverthe carnation is grown. The rot usually starts in the cortex of the stem and extends around the stem until it is girdled, the plant then wilts and dies. The rotted portion is somewhat dry and corky in nature. The fungus is soil-borne and according to Decker[18], sterilizing the soil in the bench does not control it. This is probably due to the American practice of growing the plants during the summer in open fields and moving them into green-house benches in the fall. In moving the plants a fair amount of the field soil can be expected to cling to the roots and thus impregnate the sterile bench soil with the fungus. Brown[9], at Kensington, tested a number of varieties for which growers claimed resistance. He found that all but one of the varieties proved susceptible, and varied as to the stage of maturity at which they became susceptible. The one resistant variety was of French origin; he described it as being "of poor growth and flower habit." So far as can be determined no effort was made then or subsequently to cross this variety with other commercial varieties to develop a resistant but more commercially valuable strain.

Inheritance of Doubleness

The seeds from a commercial variety of carnation selfed or crossed with another commercial variety produce what appear to be three different types of flowers. Norton[30], who first

noticed this in 1904, classified these three types as single, semi-double and double. The single is a 5-petalled flower with no commercial value (Fig. 1). The semi-double is the typical commercial florists' flower (Fig. 2). The double includes those with split calyces and monster flowers (Fig. 3), and is called double, full double, bullhead, split, or burster. For the sake of uniformity, and for reasons which will become more apparent later, the three types will be called singles, doubles, and split-doubles, throughout this paper.

Norton[30] obtained the following results from crosses of commercial varieties:

Singles	Doubles	Split-doubles
7	15	6
52	147	74

He considers this segregation to be an indication that doubleness is a simple dominant factor - the double being heterozygous; the single, homozygous recessive; and, the split-double, homozygous dominant. He[31] followed up this work by making several single X split-double crosses. The results were 249 doubles to 1 single. He concludes that "While this work does not prove that the carnation is following Mendel's law in regard to doubling, it offers evidence that anyone familiar with Mendelian hybrids would accept as satisfactory proof."

Dorner[20] who grew carnations for the commercial trade and made a large number of crosses in an endeavor to improve on the

Fig. 1 - Side and top view of a typical single.

Fig. 2 - A typical double type in bud and full bloom. This is the type which is grown commercially.

Fig. 3 - A typical split-double in bud and full bloom. The lopsided appearance caused by the split calyx makes it of little commercial value.

existing varieties reports in the same volume as Norton's later paper, that in the first year of crossing, 50% singles and 35% split-doubles were produced, but by careful selection of parents by 1906, or 15 years after the start of the work, they had reduced the number of singles to 20% "with a corresponding increase in good doubles and those having split calyces".

Batchelor(5), in 1911, made several interesting crosses, the results of which are given below:

	Number of Flowers		
	Single	Double	Split-double
Double x double	9	28	8
Single x single	32	-	-
Single x double	29	30	-
Single x split-double .	-	50	-
Double x split-double .	-	7	4

He admitted that the results appear to indicate that the carnation follows Mendel's law of dominance, but in counting the petals of the progeny he found that the average number were as follows:

	Number of Petals
Single x single	5.03
Single x double	44.30
Single x split-double	87.20
Double x split-double	130.00
Split-double x split-double . . .	183.00

Batchelor cites the findings of Dr. H. J. Webber, who continued the work started by Norton and found in crossing singles x split-doubles the following somewhat startling ratio: 5 singles: 104 doubles: 5 split-doubles. Because the singles were used as the female parent and since no blooms were bagged, the single progeny could be explained by careless technique. However this would not explain the presence of split-doubles. Batchelor is of the opinion that these apparent impurities represent the possible variations in the heterozygous form and concludes "it would seem that doubling of the carnation bloom may be dependent upon more than one set of allelomorphic factors, and that there is likely to be a certain interaction of these factors."

In 1912, Stuart[37] published the results of a number of crosses which he had made over a period of 3 years, these are summarized as follows:

	Crosses	Singles	Doubles	Split-doubles
Single x single . . .	22	354	-	-
Double x single . . .	6	21	20	-
Double x double . . .	23	62	198	
Single x split-double	44	4	988	12

His explanation of the presence of 12 split-doubles in the single x split-double crosses is: "appearance of doubleness does not necessarily indicate that the flower is a true double" and of the four singles in the same line as "a possible slight

error on the part of the operator" in pollinating. He also studied two commercial varieties which tended to split and states that the data secured would lead one to believe that these varieties were on the border-line between the double and the split-double types, and apparently some of them occasionally pass over the boundary usually supposed to be the upper limit of the double type. He apparently is satisfied, however, that his figures prove doubleness to be due to a single dominant factor.

The next paper on inheritance of doubleness was published by Saunders(35) who, although she had started the work before Norton's original paper appeared, did not complete it until 1917. She starts by stating a belief that doubling is not a simple process but is one that probably involves a number of associated changes. She tries to explain away the contradictory ratio of 5:104:5 found by Webber and cited by Batchelor(5) as "... perhaps...the presence of some stray seeds..." She concludes, however, that doubleness is due to a single dominant factor. She used English Border carnations and the greenhouse carnations for her crosses, with these results:

	Crosses	Singles	Doubles*
Singles x singles	15	170	-
Split-double x split-double .	2	-	22
Split-double x double	2	-	12

*Miss Saunders did not attempt to differentiate between doubles and split-doubles in the progeny.

	Crosses	Singles	Doubles
Single x split-double	3	-	129
Double x double	37	159	421
Double x single	1	8	10

It is interesting to note that she found in working with D. barbatus (Sweet William), that singleness was apparently due to one dominant factor, the condition thus being the reverse of that in the carnation.

No further work has been reported on the inheritance of doubleness, the subsequent workers[21,27,36] all accepting the assumption that doubleness is the expression of one dominant factor.

It can be seen from the above that doubleness in the carnation in general follows what would be expected if it were controlled by one dominant factor. In most cases, however, the populations have been relatively small and conclusions should not be drawn too hastily from them. There are discrepancies, and special emphasis is laid on the following:

	Singles	Doubles and Split-doubles
Norton[30] double x double . .	52	221
Dorner[20] double x double . .	20%	-
Batchelor (Webber)[5] single x split-double	5	109
Stuart[37] single x split-double	4	1,000

Splitting of the Calyx

The large, split-double flower already referred to is typified by multiplication and modification of the floral parts to such an extent that, in the early stages of growth, they take up more room than is available in the calyx and so burst the side of the calyx. These modifications are discussed in detail later. Some commercial varieties have a constant tendency to split; this is usually brought on by one or more of these modifications.

Ward[41] and Dorner[20] assume that splitting is entirely hereditary. But, the percentage of split flowers within a commercial variety does not remain constant from day to day or month to month, so this tendency is not entirely hereditary; environmental factors undoubtedly play a part. Connors[16] estimates that, at certain seasons of the year, some of the best varieties produce 25% or more flowers with split calyces. Szendel[39] estimates that 10% of the annual crop is lost through splitting. Flowers with split calyces are worth commercially only half as much as those with unsplit calyces[16] as the petals fall out through the split, giving the flower a lopsided appearance.

A number of workers have endeavored to determine the environmental factor or factors responsible for this variation. These will be dealt with under the various general headings which follow:

Water

Close[14] reports that variations in temperature and moisture conditions aggravate the bursting tendency. He recommends that greenhouses be so constructed as to allow a walk between the side wall and the benches because conditions cannot be controlled in a bench adjacent to the side wall. According to Connors[16], an excess of water will increase the percentage of splits, and with varieties that tend to split the percentage can be greatly reduced by keeping the plants dry. Pember[32] more recently finds that a considerable difference in soil moisture does not have any noticeable effect on splitting. This is confirmed by Beach[8] who subjected three varieties of different splitting tendencies to frequent, ordinary, and sub-normal rates of watering. He reports no significant difference in the number of splits between the three treatments within each variety.

Nutrients

Connors[16] finds that different types of soil and soil mixtures with sand have little, if any, influence on splitting; this is borne out by Weinard[44]. Connors[15], however, reports that splitting is decreased in plants grown in a sand culture on a full nutrient solution. Szendel[39] finds that applying full nutrient solution to sand at weekly intervals doubles splitting when compared with bimonthly applications at double full nutrient strength.

(a) Nitrogen

Excess: There are many conflicting results from experiments on increased rates of nitrogen. Allwood(3) claims an increase of N increases splitting. Pember(32) finds that excess N reduced splitting, even when added to such an extent that plant growth is stunted. Wheeler and Adams(48) found that increases of N increase splits with one variety and decrease them with another. Post(33) claims that an increase in N increases splits. Szendel(39) finds that increasing N gives a gradual rise in the number of splits to the point where excess N causes a decline in plant vigor, at which stage splitting decreased. Clapp and Folley(13) in a well-designed experiment, find that excess N increases splitting to a high degree.

Deficiency: Most workers claim that a deficiency of N prevents plants reaching maturity and thus no flowers form. Clapp and Folley(13) find that a N deficiency decreases splitting to a marked degree on those plants which flower.

(b) Potassium

Excess: Weinard(43) and Szendel(39) both find that an increase in K decreases the number of splits. Clapp and Folley(13) claim exactly the opposite.

Deficiency: Szendel(39) states that K deficiency does not affect splitting, whereas Clapp and Folley(13) believe that it gives a slight increase in splits.

(c) Phosphorus

Excess: Weinard and Lehenbauer[46] and Szendel[39] again agree and find that no significant difference can be found when excess P is applied. However, Clapp and Folley[13] find that it increases splits.

Deficiency: Szendel[39] finds that P deficiency completely prevents splitting and concludes that P may play an important role in the occurrence of splits. Clapp and Folley[3] find a slight decrease in splitting which is accompanied by a considerable decrease in the size of bloom and stem length.

(d) Calcium

Clapp and Folley[13] claim that Ca has no affect whatever on splitting, except that plants grown on a deficiency of Ca do not mature.

Beach[7] points out that many plants are able to satisfy their nutritional needs from solutions varying widely in composition and concentration, but that it is logical to suppose there is an optimum concentration for each element, probably in proportion to the other elements in the nutrient solution.

Light

Connors[16] states that dull weather does not seem to affect splitting to any marked degree. However, Carter[12],

Weinard[45], Laurie *et al*[26], and Weston[47] claim that dull, dark weather and lack of light at certain stages of development of the flower bud increase splitting. Holley[25] produces evidence which indicates that temperature becomes increasingly important when light intensity decreases. He claims that under low light intensities (100 to 200 candle-power), photosynthetic production may be so low that the amount of material respired easily exceeds that manufactured, thus explaining the poor production and quality of flowers obtained by careless growers.

Temperature

Baur[6], Carter[12], and Allwood[2] contend that splitting is largely caused by fluctuations in temperature. Szendel[39] subjected two varieties to a number of temperature treatments. He concludes that prolonged low temperature increases splits, and high temperature reduces splits. Heat treatment applied to plants during flower-bud formation reduces splitting. If the flower-buds are formed before or after the heat treatment, splitting is not reduced. A short, low temperature period (8-12 hours) occurring at great time intervals (2 weeks to a month apart) increases splitting significantly as compared with frequent (nightly) low temperature treatments. Close[14], as previously mentioned, reports that variation of temperature and moisture conditions aggravates the bursting tendency. The "degree of forcing" may tend to affect the splitting of the calyx[4].

Selection

Weinard[42], by selecting and propagating plants of a commercial variety which produces a high percentage of split flowers, finds that the strain improves and that by constant selection a strain that is far less subject to splitting than the normal commercial strain is developed. However, selection over several years has not entirely eliminated splitting in his plants.

Morphology of the Flower

The carnation, botanically speaking, is a single, regular, bisexual flower of the general floral formula S(5)P5A5+5G(2). The ovary is superior, made up of one locule, a free central placenta, many ovules, and 2 styles. The stamens are borne in whorls of 5, the outer whorl being superimposed to the sepals and the inner whorl to the petals. However, as previously stated, it is generally considered that there are two other types, the double, which normally has 30-60 petals or petalous structures, and the split-double or "bull-head" with 100 to 400 or more. The calyx of the latter splits at an early stage of development.

Dorner[20], in 1907, the first to venture an opinion on the cause of splitting, says that the manner in which the bloom opens is the chief factor. Batchelor[5], in 1911, considers that the number of petals is an important cause. Stuart[38], in 1912, the first to study the morphology of the

carnation flower in relation to splitting, suggests that adventitious buds may have a significant relationship to the frequency of splitting. He also notes some of the more important morphological modifications. Connors[17], 1913, in a more thorough study, cites examples of petalody of the calyx, pistils, and stamens, phyllody of the petals and ovules, median and axillary prolification of the flower, and prolification of the petals and stamens. In 1937, Szendel[40] made an intensive study of the teratology of the carnation flower. He segregates the 'abnormalities' by classifying them as deviations from (a) the ordinary arrangement, (b) the ordinary form, (c) the ordinary number, and (d) the ordinary size. This work, though very thorough and a preliminary to further study of splitting of the calyces, does not deal with the modifications as they affect splitting.

THE PRESENT EXPERIMENT

Carnation breeding has been in progress in the Division of Horticulture for the past three winters. At the commencement of the work the main purpose was to produce new varieties superior to those now under cultivation. With this in mind, and with the very limited greenhouse facilities available, only those plants with potential commercial value were retained; the others, some of which no doubt showed interesting modifica-

tions, etc., have been discarded. This is unfortunate in that the writer has not had an opportunity of personally examining most of the progeny of the crosses of the first two years. However W. S. Langton, the greenhouse operator, has kept very complete and accurate notes on these, and it is from his records that the figures making up tables 1, 2 and 3 have been taken. The experiments were not originally designed to be analysed statistically; because of this it has only been possible to apply statistical analyses to a limited extent.

Material and Technique

Plant Parents

During the first year of the work commercial varieties only were used for crossing, but, in subsequent years, seedlings which showed better characteristics were also used. Altogether, 31 commercial varieties and 35 seedlings have been successfully used as parents. A total of 554 crosses have been made of which 233 have set seed, and 2,427 seedlings have been raised.

Appendix 'A' lists the commercial varieties and seedlings used as parents. Opposite each is a code number which, for convenience and economy of space, are used for reference in the tables and text.

Propagation

Both heel and top cuttings were taken. The populations of any one variety were small (8-10 per year) and no effort

has been made to see if differences between the two types of cuttings exists. The number of strikes has always been highly satisfactory, approaching 100 percent in most cases.

Pollination

The carnation is protandrous, the anthers dehiscing 2-4 days before the stigmas are receptive, thus making it relatively simple to prevent self pollination. Dorner[20] recommends that the inner petals of the flower be removed to facilitate removal of the anthers. However, it was found simpler and surer to split the calyx completely in 3 or 4 places the day the first petals pushed free of the calyx. The petals fall away from the centre, leaving the ovary and anthers free. The anthers are then readily removed and one can be positive that none remain. Two to four days later the stigmas signify their receptivity by becoming raised from the surface of the style, giving it a hairy appearance. The pollen is transferred from the male parent by selecting a recently ruptured anther, severing its filament with a pair of pointed forceps and carrying it intact to the female and rubbing the anther over the stigmas of the latter. The forceps are thoroughly cleaned between each operation. Neither the male nor female parent has been bagged, but as all plants are grown in the greenhouse which is frequently and carefully fumigated and sprayed, the opportunity for chance pollination is very slight.

Some varieties do not produce pollen, e.g. #13; here the androecium is completely suppressed. In others, at certain seasons, no pollen or very little pollen is produced. It is quite possible that the receptivity of the stigmas is also affected during these periods.

Numbering of Selections

The first two figures give the year of the cross, the next two or three the number of the cross. A plant selected from any cross for further study receives a letter after these numbers, commencing with A. Thus, 4394-B is the second plant (b) selected from those resulting from the ninety-fourth cross made in 1943.

Seed Production

Table 1 gives the number of crosses and takes, the average number of seeds and seedlings per take, classified as to the length of day during which crossing was done.

Table 1. The Number of Crosses and Takes, and the Number of Seeds and Seedlings Produced in Relation to the Number of Daylight Minutes per Day.

Period of Year (a)	Av. No. of Mins. Daylight per day(11) (b)	Crosses (c)	Takes (d)	% Takes: Crosses (e)	Av. No. Seeds/ Take (f)	Av. No. Seedlings/ Take (g)	% Germination (h)
Mar.8-Apr.3 and Sep.11-Oct.8	730	91	52	57.1	28.7	12.9	44.9
Feb.21-Mar.7 and Oct.9-Oct.23	640	50	24	48	30.6	9.5	31.0
Jan.22-Feb.20 and Oct.24-Nov.21	550	128	46	35.9	19.2	10.2	53.1
Nov.22-Jan.21	460	209	58	27.7	18.5	11.4	61.6
		478	180				

Analyses of the results, using the formula for simple correlation(109), shows that

$$r_{be} = .997^{**}$$

$$r_{bf} = .865^{*}$$

$$r_{bg} = .335$$

$$r_{bh} = -.717$$

From this it can be concluded that an increase in the length of day will increase the number of successful crosses, and increase the number of seeds per capsule.

Graphic representations of these results are shown in Figs. 4 and 5.

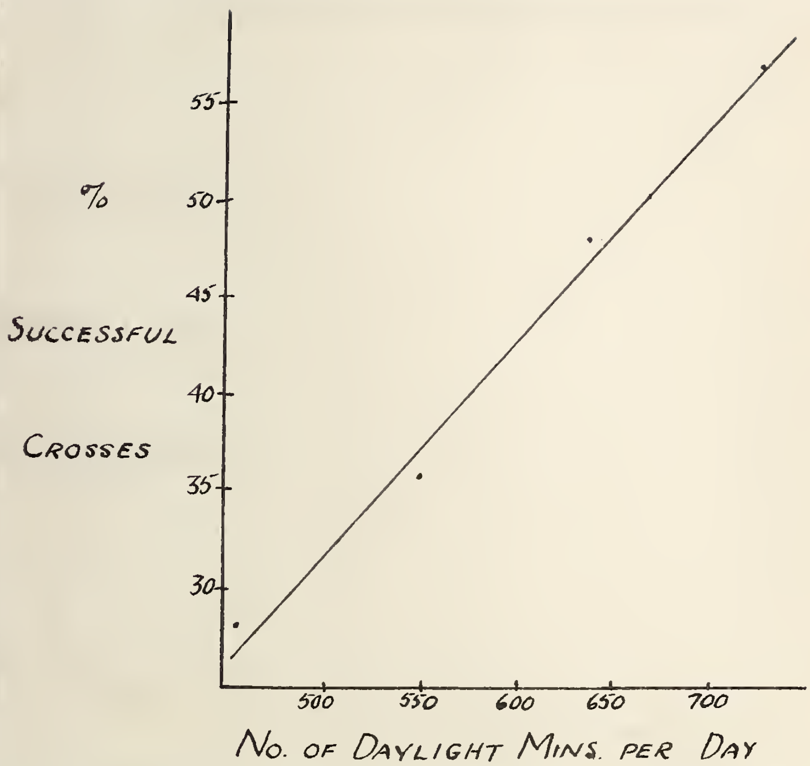

Fig. 4 - Relation Between Length of Day and Percentage of Successful Crosses.

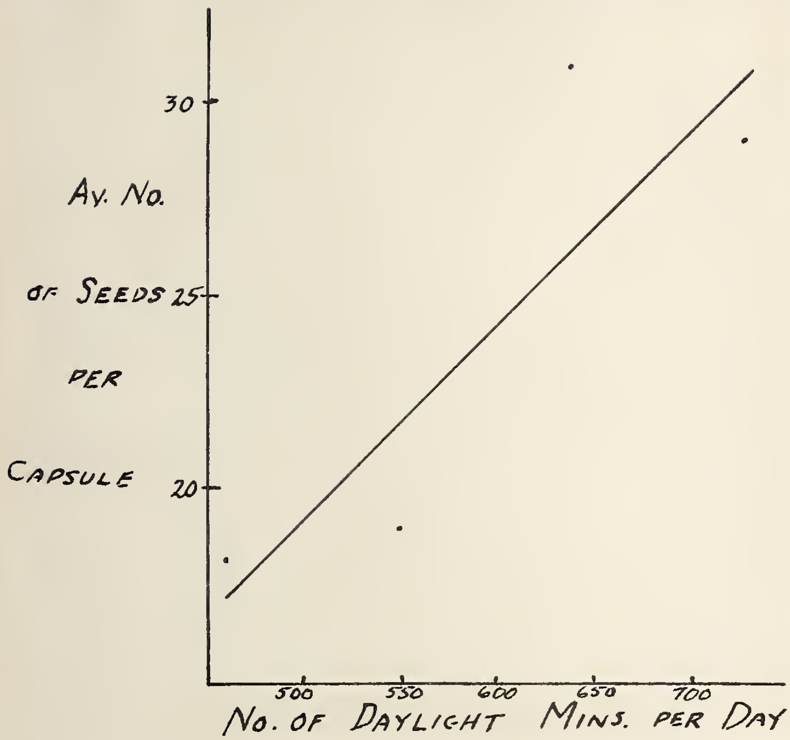

Fig. 5 - Relation Between Length of Day and Number of Seeds Per Capsule.

Inheritance

Inheritance of Abnormal Types

A careful check was not kept of the progeny of any of the crosses during the early seedling stages so it is impossible to state whether the lethal types mentioned by Mehlquist(28) appeared. However several examples of his so-called stocky type, and a few annual types have appeared. The stocky type has arisen from crosses involving a number of well known commercial varieties but as the notes kept are not complete in this regard, conclusions cannot be drawn from them at this time.

Inheritance of Disease Resistance

(a) Stem Rot

This disease was not encountered and mention of it under the literature review was made only to point out the possibility of breeding resistant varieties.

(b) Carnation Rust

Much variation in susceptibility to this disease has been observed. Some varieties are very susceptible; others have shown apparent resistance. However, as the experiment depended primarily on the production of blossoms, rust was not encouraged. Plants were not tested by inoculating them with the rust so, although some varieties have been selected showing apparent resistance, no attempt at drawing conclusions from the present results will be made here.

Inheritance of Doubleness

Most of the crosses have been double x double. A few single x split-double crosses have been made. Table 2 gives the crosses of double x double, with the progeny classified as to singles, doubles and split-doubles. Table 2(b) summarizes Table 2(a) by totalling the progeny of each parent when it was used as a male, and also as a female.

Table 2(a). Crosses of Double x Double with Progeny Segregated as to Singles, Doubles, and Split-doubles.

Female Parent	Male Parent	No. of Crosses	Singles	Doubles	Split-Doubles	Male Parent	Female Parent	No. of Crosses	Singles	Doubles	Split-Doubles
1	various	8	-	-	-	1	9	2	4	25	8
							13	1	-	9	-
							22	3	9	19	8
							26	2	-	2	2
							29	1	-	1	-
							32	2	4	9	9
							various	16			
2	3	2	5	10	5	2	various	4			
	6	1	4	5	2						
	11	1	4	5	4						
	23	1	-	3	2						
	32	1	-	1	1						
	49	1	1	1	2						
	various	7									
3	4	1	-	1	-	3	2	2	5	10	5
	9	2	1	6	1		7	1	-	6	2
	10	2	7	5	6		10	1	2	4	3
	11	1	-	2	1		12	1	-	-	1
	14	2	16	29	2		13	1	-	20	-
	22	1	1	-	-		14	1	1	6	2
	28	1	1	5	-		32	2	3	9	5
	46	1	4	5	1		various	9			
	48	1	-	1	-						
	45	1	2	3	1						
	50	1	1	1	1						
	53	1	7	7	3						
	various	39									

Table 2(a) Cont'd

Female Parent	Male Parent	No. of Crosses	Singles	Doubles	Split-Doubles
4	various	4			
5	10	1	-	14	7
	26	1	-	1	-
	31	1	2	5	2
	34	1	-	38	22
	47	1	-	8	6
6	10	2	2	5	2
	18	2	1	6	4
	30	1	-	-	1
	50	1	5	6	1
	various	2			
7	3	1	-	6	2
	26	1	-	6	5
	42	1	1	-	3
	various	9			
8	11	1	1	5	3
	15	1	-	3	4
	various	3			
9	1	2	4	25	8
	10	1	1	1	1
	24	1	-	11	4
	28	2	8	23	6
	32	2	13	35	7
	45	1	-	10	1
	various	7			

Male Parent	Female Parent	No. of Crosses	Singles	Doubles	Split-Doubles
4	3	1	-	1	-
	26	1	4	8	2
	various	2			
5	various	2			
6	2	1	4	5	2
	various	4			
7	31	1	-	2	1
	various	12			
8	14	1	7	6	3
	15	1	-	12	6
	17	1	4	5	1
	30	1	4	8	3
	44	1	-	15	8
	various	3			
9	3	2	1	6	1
	13	1	-	-	1
	14	3	12	28	12
	21	1	6	19	4
	22	1	1	3	5
	23	1	15	8	10
	25	1	1	7	1

Table 2(a) Cont'd

Female Parent	Male Parent	No. of Crosses	Singles	Doubles	Split-Doubles
10	3	1	2	4	3
	10	1	3	4	3
	11	1	2	-	-
	19	1	-	3	1
	26	1	1	2	-
	28	1	6	12	8
	31	1	1	1	1
	47	1	-	2	-
	various	8			
11	10	1	-	5	6
	26	1	-	1	1
	40	1	1	1	3
	42	1	2	6	8
	various	33			
12	3	1	-	-	1
	various	1			

Male Parent	Female Parent	No. of Crosses	Singles	Doubles	Split-Doubles
9 cont'd	26	1	-	7	4
	30	2	8	16	8
	32	1	-	1	-
	various	26			
10	3	2	7	5	6
	5	1	-	14	7
	6	2	2	5	2
	9	1	1	1	1
	10	1	3	4	3
	11	1	-	5	6
	17	1	2	-	3
	25	1	2	2	2
	26	1	-	-	2
	28	1	5	9	6
	37	1	2	7	7
	41	1	-	1	-
	various	11			
11	2	1	4	5	4
	3	1	-	2	1
	8	1	1	5	3
	10	1	2	-	-
	22	1	10	12	14
	30	2	6	6	3
	32	1	-	2	1
	various	20			
12					

Table 2(a) Cont'd

Female Parent	Male Parent	No. of Crosses	Singles	Doubles	Split-Doubles	Male Parent	Female Parent	No. of Crosses	Singles	Doubles	Split-Doubles
13	1	1	-	9	-	13	(no pollen)				
	3	1	-	20	-						
	9	1	-	-	1						
	14	1	-	12	4						
	26	2	-	6	-						
	32	4	1	19	14						
	various	9									
14	3	1	1	6	2	14	3	2	16	29	2
	8	1	7	6	3		13	1	-	12	4
	9	3	12	28	12		14	1	3	4	1
	14	1	3	4	1		22	1	5	9	3
	26	1	-	21	4		26	1	-	1	-
	32	2	9	22	11		30	2	4	21	8
	42	1	-	1	-		32	1	3	5	-
	various	4					various	10			
15	8	1	-	12	6	15	8	1	-	3	4
	38	2	-	5	2		various	1			
	various	2									
16	37	1	-	6	3	16	28	1	-	1	3
	various	14					40	1	-	1	2
							55	1	-	2	1
							various	3			
17	8	1	4	5	1	17					
	10	1	2	-	3						
	various	7									
18						18	6	2	1	6	4
							31	1	-	1	-
							various	7			
19	various	13				19	10	1	-	3	1
							21	2	3	3	4
							various	6			

Table 2(a) Cont'd

Female Parent	Male Parent	No. of Crosses	Singles	Doubles	Split-Doubles	Male Parent	Female Parent	No. of Crosses	Singles	Doubles	Split-Doubles
20	various	1				20	37	1	-	15	1
							various	4			
21	9	1	6	19	4	21					
	19	2	3	3	4						
	various	5									
22	1	3	9	19	8	22	3	1	1	-	-
	9	1	1	3	5		22	1	2	28	3
	11	1	10	12	14		various	8			
	14	1	5	9	3						
	22	1	2	28	3						
	24	1	-	23	9						
	26	1	-	13	15						
	28	1	6	9	8						
	31	1	-	-	1						
	45	1	4	6	2						
	53	1	7	11	6						
	various	18									
23	9	1	15	8	10	23	2	1	-	3	2
	23	1	2	6	2		23	1	2	6	2
	33	1	6	21	7		various	1			
	36	1	-	1	-						
	various	2									
24	24	1	-	-	1	24	9	1	-	11	4
	various	4					22	1	-	23	9
							24	1	-	-	1
							26	1	2	11	1
							30	1	-	1	3
							various	2			

Table 2(a) Cont'd

Female Parent	Male Parent	No. of Crosses	Singles	Doubles	Split-Doubles
25	9	1	1	7	1
	10	1	2	2	2
	35	1	-	1	-
	54	1	1	-	-
	various	2			
26	1	2	-	2	2
	4	1	4	8	2
	9	1	-	7	4
	10	1	-	-	2
	14	1	-	1	-
	24	1	2	11	1
	28	1	-	22	1
	31	2	-	18	12
	32	1	-	1	-
	43	1	-	1	-
	various	16			
27	28	1	1	4	6
	30	2	9	24	13
	51	1	-	1	-
	various	5			
28	10	1	5	9	6
	16	1	-	1	3
	26	1	-	4	2
	28	1	-	-	1
	56	1	-	2	7
	various	17			

Male Parent	Female Parent	No. of Crosses	Singles	Doubles	Split-Doubles
25	various	2			
26	5	1	-	1	-
	7	1	-	6	5
	10	1	1	2	-
	11	1	-	1	1
	13	2	-	6	-
	14	1	-	21	4
	22	1	-	13	15
	28	1	-	4	2
	30	1	-	5	5
	various	33			
27	various	1			
28	3	1	1	5	-
	9	2	8	23	6
	10	1	6	12	8
	22	1	6	9	8
	26	1	-	22	1
	27	1	1	4	6
	28	1	-	-	1
	31	1	-	-	2
	various	8			

Table 2(a) Cont'd

Female Parent	Male Parent	No. of Crosses	Singles	Doubles	Split-Doubles	Male Parent	Female Parent	No. of Crosses	Singles	Doubles	Split-Doubles
29	1	1	-	1	-	29	various	20			
	various	18									
30	8	1	4	8	3	30	6	1	-	-	1
	9	2	8	16	8		27	2	9	24	13
	11	2	6	6	3		various	11			
	14	2	4	21	8						
	24	1	-	1	3						
	26	1	-	5	5						
	32	1	-	1	-						
	various	5									
31	7	1	-	2	1	31	5	1	2	5	2
	18	1	-	1	-		10	1	1	1	1
	28	1	-	-	2		22	1	-	-	1
	39	1	4	2	-		26	2	-	18	12
	47	1	1	4	2		42	1	-	2	-
	49	1	2	3	2		various	29			
	various	14									
32	1	2	4	9	9	32	2	1	-	1	1
	3	2	3	9	5		9	2	13	35	7
	9	1	-	1	-		14	2	9	22	11
	11	1	-	2	1		13	4	1	19	14
	14	1	3	5	-		26	1	-	1	-
	32	1	-	2	-		30	1	-	1	-
	various	6					32	1	-	2	-
							various	20			
33						33	23	1	6	21	7
							various	1			

Table 2(a) Cont'd

Female Parent	Male Parent	No. of Crosses	Singles	Doubles	Split-Doubles	Male Parent	Female Parent	No. of Crosses	Singles	Doubles	Split-Doubles
34						34	5 various	1 2	-	38	22
35	various	2				35	25 various	1 1	-	1	-
36						36	23 various	1 1	-	1	-
37	10 20	1 1	2 -	7 15	7 1	37	16	1	-	6	3
38	various	2				38	15	2	-	5	2
39	various	1				39	31	1	4	2	-
40	16 various	1 3	-	1	2	40	11 various	1 4	1	1	3
41	10	1	-	1	-	41	various	1			
42	11 31 various	1 1 1	1 -	- 2	1 -	42	7 11 14 various	1 1 1 2	1 2 -	- 6 1	3 8 -
43						43	26	1	-	1	-
44	8	1	-	15	8	44					
45	45	1	4	9	-	45	3 9 22 45	1 1 1 1	2 - 4 4	3 10 6 9	1 1 2 -

Table 2(a) Cont'd

Female Parent	Male Parent	No. of Crosses	Singles	Doubles	Split-Doubles	Male Parent	Female Parent	No. of Crosses	Singles	Doubles	Split-Doubles
46	46	1	-	2	-	46	3 46 various	1 1 2	4 -	5 2	1 -
47	48	1	2	12	1	47	5 10 31 various	1 1 1 2	- - 1	8 2 4	6 - 2
48	48	1	5	13	-	48	3 47 48 various	1 1 1 1	- 2 5	1 12 13	- 1 -
49	various	1				49	2 31 57 various	1 1 1 5	1 2 -	1 3 1	2 2 -
50	various	1				50	3 6	1 1	1 5	1 6	1 1
51						51	27	1	-	1	-
52	52	1	-	2	-	52	52	1	-	2	-
53	various	3				53	3 22	1 1	7 7	7 11	3 6
54						54	25	1	1	-	-
55	16	1	-	2	1	55					
56						56	28	1	-	2	7
57	49	1	-	1	-						

Table 2(b). A Summary of Table 2(a)

Female Parent	No. of Crosses	No. of Takes	Total Singles	Total Doubles	Total Split-Doubles	Male Parent	No. of Crosses	No. of Takes	Total Singles	Total Doubles	Total Split-Doubles
1	8	-	-	-	-	1	27	11	17	65	27
2	14	7	14	25	16	2	4	-	-	-	-
3	54	15	40	65	16	3	18	9	11	55	18
4	4	-	-	-	-	4	4	2	4	9	2
5	5	5	2	66	37	5	2	-	-	-	-
6	8	6	8	17	8	6	5	1	4	5	2
7	12	3	1	12	10	7	13	1	-	2	1
8	5	2	1	8	7	8	8	5	15	46	21
9	16	9	26	105	27	9	40	14	44	95	46
10	16	8	15	28	16	10	25	14	24	53	45
11	37	4	3	13	18	11	29	9	24	32	27
12	2	1	-	-	1	12	-	-	-	-	-
13	19	10	1	66	19	13	-	-	-	-	-
14	14	10	32	88	33	14	19	9	31	81	18
15	5	3	-	17	8	15	2	1	-	3	4
16	15	1	-	6	3	16	6	3	-	4	6
17	9	2	6	5	4	17	-	-	-	-	-
18	-	-	-	-	-	18	10	3	1	7	4
19	13	-	-	-	-	19	9	3	3	6	5
20	1	-	-	-	-	20	5	1	-	15	1
21	8	3	9	22	8	21	-	-	-	-	-
22	31	13	44	133	74	22	10	2	3	28	3
23	6	4	23	36	19	23	3	2	2	9	4

Table 2(b) Cont'd

Female Parent	No. of Crosses	No. of Takes	Total Singles	Total Doubles	Total Split-Doubles	Male Parent	No. of Crosses	No. of Takes	Total Singles	Total Doubles	Total Split-Doubles
24	5	1	-	-	1	24	7	5	2	46	18
25	6	4	4	10	3	25	2	-	-	-	-
26	28	12	6	71	24	26	43	10	1	59	32
27	9	4	10	29	19	27	1	-	-	-	-
28	22	5	5	16	19	28	17	9	22	75	32
29	19	1	-	1	-	29	20	-	-	-	-
30	15	10	22	58	30	30	14	3	9	24	14
31	20	6	7	12	7	31	35	6	3	26	16
32	14	8	10	28	15	32	32	12	23	81	33
33	-	-	-	-	-	33	2	1	6	21	7
34	-	-	-	-	-	34	3	1	-	38	22
35	2	-	-	-	-	35	2	1	-	1	-
36	-	-	-	-	-	36	2	1	-	1	-
37	2	2	2	22	8	37	1	1	-	6	3
38	2	-	-	-	-	38	2	2	-	5	2
39	1	-	-	-	-	39	1	1	4	2	-
40	4	1	-	1	2	40	5	1	1	1	3
41	1	1	-	1	-	41	1	-	-	-	-
42	3	2	1	2	1	42	5	3	3	7	11
43	-	-	-	-	-	43	1	1	-	1	-
44	1	1	-	15	8	44	-	-	-	-	-
45	1	1	4	9	-	45	4	4	10	28	4
46	1	1	-	2	-	46	4	2	4	7	1
47	1	1	2	12	1	47	5	3	1	14	8

Table 2(b) Cont'd

Female Parent	No. of Crosses	No. of Takes	Total Singles	Total Doubles	Total Split-Doubles	Male Parent	No. of Crosses	No. of Takes	Total Singles	Total Doubles	Total Split-Doubles
48	1	1	5	13	-	48	4	3	7	26	1
49	1	-	-	-	-	49	8	3	3	5	4
50	1	-	-	-	-	50	2	2	6	7	2
51	-	-	-	-	-	51	1	1	-	1	-
52	1	1	-	2	-	52	1	1	-	2	-
53	3	-	-	-	-	53	2	2	14	18	9
54	-	-	-	-	-	54	1	1	1	-	-
55	1	1	-	2	1	55	-	-	-	-	-
56	-	-	-	-	-	56	1	1	-	2	7
57	1	1	-	1	-	57	-	-	-	-	-
Total	469	172	303	1019	463		469	172	303	1019	463

These results do not approximate the 1:2:1 ratio expected from crosses of types heterozygous for one dominant factor.

Special attention is directed to the progeny of parents #3, #11, and #53; these show, in most cases, a higher number of singles to doubles than is expected in a 1:2:1 ratio. Also notice the results of crosses involving varieties #5, #7, #13, #15, #16, #24, and #26; here the progeny are preponderantly double. These last mentioned, although producing some split flowers, are amongst the most popular commercial varieties. The average petal count of these varieties, with the exception of #5 is between 60 and 75. #5 averages 35 petals. None of these varieties show adventitious buds.

Table 3. Crosses of Singles x Split-doubles with Progeny Segregated as to Singles, Doubles, and Split-doubles.

Female Parent	Male Parent	No. of Crosses	Singles	Doubles	Split-Doubles	Male Parent	Female Parent	No. of Crosses	Singles	Doubles	Split-Doubles
58	65	1	-	7	-	61	63	1	-	25	3
59	61	1	1	2	-	61	59	1	1	2	-
60	62	1	-	2	-	62	60	1	-	2	-
63	61	1	-	25	3	65	58	1	-	7	-
64	66	1	15	8	1	66	64	1	15	8	1
Total		5	16	44	4			5	16	44	4

If doubleness is the expression of one dominant factor the progeny should, of course, have been entirely doubles.

The discrepancy that can be noted between the total number of crosses and takes shown in Tables 2 and 3, and that shown in Table 1, is due to a few crosses of unknown parentage.

Splitting of the Calyx

Splitting of Calyces of Varieties that Normally do not Split

It has been noted throughout this experiment that varieties which normally do not split can be forced to split by rapid fluctuation in temperature. Whether this induces a larger number of floral parts, or whether it is the way the petals develop in relation to the calyx, has not been determined. The population of any one variety has been very small (8-10 plants each season) so conclusions on this phase cannot be drawn from the work thus far.

Morphological Modifications as they Affect Splitting

This study will treat each type of floral part separately, note the modifications to which it is susceptible, and consider those that affect splitting. It is based on observations made in examining 200 flowers. Fig. 6 shows a longitudinal section of a single flower; all parts of the flower are visible but the androecium which was rudimentary.

Fig. 6 - A longitudinal ~~cross~~-section of a typical single showing most of the floral parts. Unfortunately, the androecium is rudimentary in this specimen, so it is not visible.

Bracts. These appear in alternating opposite pairs on the outside, at the base of the calyx. The number of pairs varies from 1 to 4, the normal number being 3. As their growth up the side of the calyx is usually limited to about $\frac{1}{4}$ inch, it is not considered that they are a factor in preventing splitting.

Sepals. The calyx is made up of 5 sepals which are fused at the base and for approximately 4/5 of their length, only the triangular tip of each being separate. The sepals vary somewhat in length, the average being about $1\frac{1}{4}$ inches. They are normally fused for about 1 inch of their length.

(a) Calycanthemy, or petalody of the calyx, was noted by Connors[17], but was not observed in the flowers examined here.

(b) Multiplication of the sepals: No complete doubling, or extra whorl of the sepals was observed, although a partial whorl of 3 sepals, separate but adjacent, has been found inside the normal calyx. There is an infrequent occurrence of one additional sepal; this is usually fused with the rest of the calyx, in one case, it was separate and outside the calyx, and, in another, it was separate and immediately inside the calyx. The latter may be an example of phyllody of a petal, but it was a perfectly formed sepal only slightly shorter than those in the calyx and was assumed to be due to multiplication of the calyx.

(c) Reduction in the number of sepals has been observed in a few flowers where the calyx was made up to 4 sepals.

Multiplication of the sepals, occurring inside the calyx, will cause splitting but as this occurs infrequently it is not an important factor. The other modifications of the calyx do not appear to affect splitting.

Corolla. The petals normally have a narrow basal structure, about 1/8 inch across and 1 inch long. The blade of the petal is variable in size, its width ranging from $\frac{1}{4}$ to $2\frac{1}{2}$ inches, and its length from $\frac{1}{2}$ to 2 inches.

(a) Multiplication: Worsdell(49) says that one of the causes of double flowers "is division of the petals at an early stage of their development; if the division takes place collaterally there will be an increase in the numbers of the whorl; if it occurs serially, i.e. in the antero-posterior plane, the number of whorls will be increased". In the double carnation it appears that both types of division occur, as in the outer whorl the number of petals is usually 10 to 12. The number of whorls is sometimes as high as 7.

(b) Fission: All grades of fission, from serrated to cleft, have been noted in the petal. The fission normally occurs in the middle of a petal; this is undoubtedly an indication of division as noted above. Not infrequently fission occurs on one side of the petal giving it a lobed

appearance. Fig. 7 shows the petals of a normal double in which some examples of fission can be observed. Fig. 8 shows fission of the two types mentioned in (a) above.

(c) Phyllody: This occurs occasionally. It is usually expressed in a thickened green 'midrib' extending up the centre of the petal. The extra sepal noted (page 50) may be an example of complete phyllody of a petal.

(d) Cohesion: This was noted by Connors[17] as a tubular construction consisting of two petals. However, in the present study this has not been encountered.

In general, considering the corolla, splitting may be induced by a large number of petals, and by a medium number of large petals. Phyllody, causing petals to be thicker and less flexible, may also bring about splitting, but as it appears only occasionally it is not a common cause.

Androecium. The androecium is subject to many variations. Normally it consists of 10 stamens. The filaments vary somewhat in length, but when fully developed range from 1 to $1\frac{3}{4}$ inches. Each is surmounted by a versatile anther.

(a) Petalody of the stamens: This is very common. The amount of petal development varies all the way from a fully formed petal which cannot be differentiated from a true petal, to a filament surmounted by a very thin, colorless, petalous structure about $\frac{1}{4}$ inch wide by 1/3

Fig. 7 - The petals of a typical double flower. This is the dissection of the flower in Fig. 2.

Fig. 8 - Fission of petals: Collateral fission (top, left); fission occurring serially (centre and top, right).

to $\frac{1}{2}$ inch high. All intermediate sizes and forms appear. Normally the anther is first affected, but examples have been found where the filament has become petalous and attached to the petalous formation is an anther which sometimes contains pollen. Viability tests of this pollen, however, have not been carried out. Worsdell(49) points out that in Clematis, petalody is due to expansion of the filament, in Ranunculus it arises from dilation of the anther, in Helleborus the petals arise from both filament and anther, and in Camellia all three types occur on the same plant. From the present study it appears that the carnation like the Camellia displays all three types. Fig. 9 shows some of the intermediate forms.

(b) Multiplication: The number of stamens in singles is always twice the number of petals; even when the flower has the unusual number of 6 petals, there are 12 stamens. Doubles vary in the number of stamens they possess; only rarely are 10 found, the average is approximately 20, but as high as 30 have been counted. On the doubles that show more than 10 stamens there are usually examples of petalous stamens, however, which makes determination of the true number impossible. There appears to be a limit to the number of stamens produced without petalous tendencies. The number of petals and petalous organs

Fig. 9 - Some of the intermediate stages in petalody of the stamens.

that arise from the receptacle appears to be limited to between 70 and 80. The remainder of the petals arise from adventitious buds (see page 62). Worsdell[49] considers that the main cause of doubling in flowers is due to division of the staminal rudiments and subsequent petalody of some or all of the products. Undoubtedly some cases of split calyces are caused by these two factors.

Gynoecium. The ovary is elliptical in shape, being broader at the base. It is usually about ½ to 3/4 inch high and ¼ to ½ inch wide at its broadest part. It is surmounted by 2 or more thin styles normally an inch to 1½ inches long. These are slightly curved outwards near the apex and are usually white although some adopt the color of the petal. The stigma is evidenced by a narrow band of hair-like growths on the inner side of the style, running almost its entire length. When the stigma is mature, the ends of these hairs protrude from the surface of the style, giving it a roughened, hairy appearance. There are numerous ovules borne on a free-central placenta. It is interesting to note that though the placenta is called free-central, the apex of the placenta is joined to the apex of the ovary, and thus to the styles, by thin, rough-surfaced, white, thread-like structures, normally 2 in number. These are probably the rudiments of a once axial placenta. They may be the junction of the styles to the placenta through which

the pollen tubes pass. In some cases, these structures do not appear but their rudiments are present. These can be seen in Fig. 6.

(a) Petalody of the carpel:

(i) Petalody of the ovary: Only once was this observed; the placenta was rudimentary, bearing no ovules, and the ovary was entirely open along one side, making it somewhat leaf-like in appearance. In color, it was mostly green but the parts near the opening were white.

(ii) Petalody of the styles: This occurs with fair frequency, usually being found as short, broad, white structures arising near the base of the style. Sometimes the hairs of the stigma protrude in a cluster which, on a cursory inspection, might be taken for an example of petalody. Connors(17) appears to have made this mistake.

(iii) Petalody of the ovules: Two examples of this have been seen. In one the apex of the ovary was open and somewhat like the calyx in shape; three very short rudimentary styles were present. Ten full sized petalous structures arose from the base of the ovary where the placenta is normally seated. These petals pushed right through the open top of the ovary. The other example is no doubt an example

of median prolification. Here the ovary was large, had two apparently normal styles, the ovary wall at the base was ruptured, and inside could be seen another green structure. On dissection it was found that this green structure was a sepal, part of a complete calyx. Inside the calyx were numerous closely packed petals, a few short rudimentary anthers, and a small rudimentary ovary with two short colorless styles.

(b) Carpellody of the ovule: This is a common occurrence. The ovule forms a rudimentary, small ovary surmounted by a long style. The style usually attempts to force itself through the micropyle at the apex of the parent ovary. As many as 10 of these carpels have been found in one parent ovary. When this modification is present the parent ovary is full, round and slightly larger than normal. Carpellody of the ovule is normally accompanied by an increase in the number of styles on the parent ovary. Table 4 shows the occurrence of carpellous ovules and number of styles of 122 flowers taken at random.

Table 4. Number of Styles Present when Carpellous Ovules are Present in Ovary as Compared with Normal Ovary.

No. of Styles (a)	Flowers with Carpellous Ovules (b)	Flowers with Normal Ovaries (c)	% Flowers with Carpellous Ovules (d)
2	3	45	6.25
3	6	47	11.32
4	6	12	33.33
5	2	1	66.67

On analysis of these results for simple correlation, it was found that $r_{ad} = .954^{**}$. So there is a highly significant correlation between the presence of carpellous ovules and an increase in the number of styles. A graphic representation of this is shown in Fig. 10.

Occasionally, when only one ovule on the placenta becomes carpellate it produces a placenta of its own on which are a few ovules. This is always at the expense of most of the other ovules on the parent placenta. Worsdell[49], referring to this modification in Primula, observed that, considering the ovule as a structure evolved from a leaflet, it would seem quite possible for the ovule to develop into an independent leaf equal in size and similar in construction to the leaf of which it is a part. Carpellody of the ovule has not been observed in single flowers.

(c) Suppression: Complete suppression of the carpel has not been observed, all flowers having, from outward appearances, normal ovaries and styles. However, suppression of the placenta does occur, it then being shortened, shrivelled and brownish in color. If it bears any ovules, they are small, shrivelled and transparent.

The only abnormalities of the gynoecium which may affect splitting are: carpellody and petalody of the ovules. But, as neither appears with great frequency, they are not considered of particular importance.

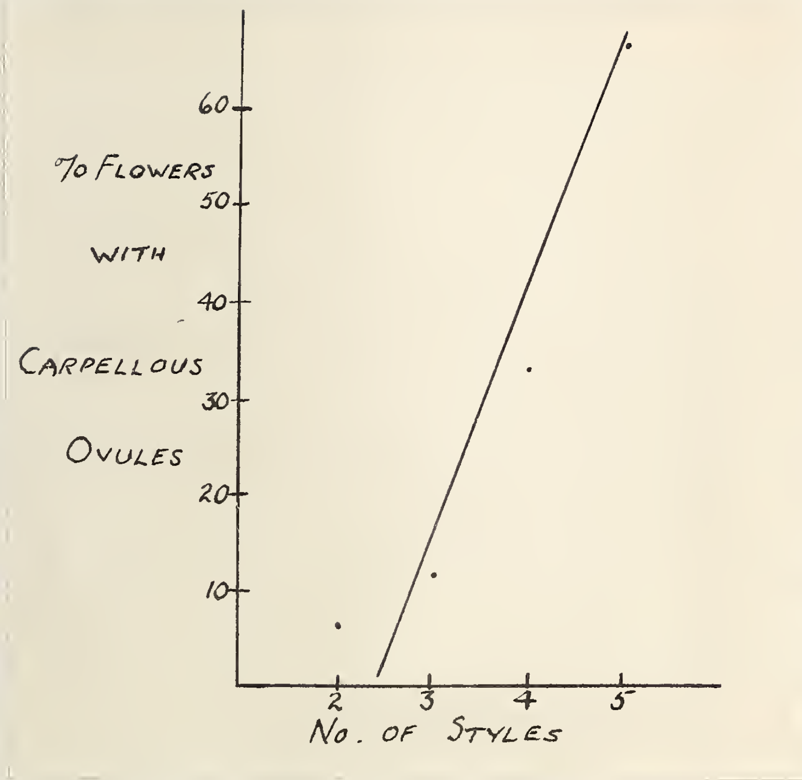

Fig. 10 - The Occurrence of Carpellous Ovules and Increase in the Number of Styles.

<u>Adventitious Buds</u>. These appear with surprising frequency and in several forms. They arise apparently from the axils of petals, although this is difficult to ascertain due to the large number of petals in the flowers. Connors(17) considers that they arise as deviations of the androecium, but Worsdell(49) claims they are axillary prolifications. They are borne on a stalk or stem-like structure and appear in these forms:

(a) A short stem about $\frac{1}{4}$ inch long from which arise 3 to 8 petal-like structures being terminated by one of these. The "petals" adopt the color of the true petals of the flower.

(b) A somewhat longer stem, $\frac{1}{4}$ to $\frac{3}{4}$ inch long, carrying from 8 to 20 petalous structures on its stem, and terminating in a growing point encased in small green or colorless petalous structures. Occasionally the growing point is protected by one or more pairs of thick, green, leaf-like appendages about $\frac{1}{4}$ inch long. The larger "petals" are colored like the normal petals of the flower.

(c) A stalk the same length as (b) but devoid of petals and terminating in one or two rudimentary carpels. This may be an expression of doubling, or prolification, of the carpel.

Toward the base of the stem of all three types a stamen or rudimentary stamen frequently appears. In counting petals and considering the petalous structures in these adventitious

buds as petals, the number of petals of some flowers is amazingly high, as many as 200 being counted on one flower. Batchelor(5) counted one with 425. The number of adventitious buds to a flower varies from 1 to 15. No singles with adventitious buds have been observed. Figs. 11, 12, 13, 14, and 15 show the adventitious buds of one flower. Table 5 shows the appearance of adventitious buds in flowers with split calyces Undoubtedly they are the most common cause of splitting.

Table 5. Occurrence of Adventitious Buds in Split and Unsplit Carnation Flowers.

No. of petals and petalous structures	No. of flowers examined	No. of flowers with adventitious buds	Av. No. of adventitious buds per flower	Av. No. of petals per adventitious buds	No. of flowers without adventitious buds
Split					
50- 69	19	10	1.64	6.77	9
70- 89	15	12	1.92	6.21	3
90-109	6	6	1.83	11.11	-
110-129	8	8	5.75	8.81	-
130-149	8	8	5.50	14.50	-
150-up	3	3	8.00	12.43	-
Unsplit					
10-19	1	-	-	-	1
20-29	10	-	-	-	10
30-39	21	-	-	-	21
40-49	14	1	1	8	13
50-59	4	1	1	6	3
60-69	3	-	-	-	3
70-79	1	-	-	-	1

Fig. 11 - A typical split-double. Figs. 12, 13, 14, and 15 are photographs of parts of this particular flower.

Fig. 12 - The flower photographed in Fig. 11, showing one of its adventitious buds.

Fig. 13 - The same flower as in Fig. 11 but with sepals and petals removed to show the adventitious buds.

Fig. 14 - The petals and petalous structures of the flower shown in Fig. 11. The bottom row and the three structures on the extreme right of the second bottom row are adventitious buds.

Fig. 15 - The three top rows are three of the adventitious buds shown in Fig. 14, dissected to show the various structures.

The maximum number of petals and petalous structures arising from the base of the receptacle is between 70 and 80. All the other petalous structures originate on the adventitious buds (with the rare exceptions of petalous ovules). A few commercial varieties have average petal counts of 60 to 75, as noted on page 46. Their progeny indicate a high degree of doubleness in the parent.

The presence of adventitious buds is probably the most common cause of splitting.

In the order in which they affect splitting of calyces, these modifications are arranged as follows:

1. Adventitious buds.
2. Multiplication and petalody of the stamens.
3. Multiplication of the petals.

Of course the appearance of only one of these modifications is rare. One flower usually shows signs of more than one modification, so it is difficult to ascertain which is primarily responsible for splitting.

There are several other modifications such as increase or reduction in the number of sepals, petalody of the sepals, etc., which also affect splitting, but these appear so infrequently that they are not important factors.

DISCUSSION

The results shown in Table 1 and analyses of these results indicate that:

With an increase in the length of day, an increase in the number of successful crosses and the number of seeds per capsule can be expected. From this it is suggested that the best results will be obtained by breeding during the summer months. This, after all, is logical, because, even though the plants grow longer stems and more commercially desirable flowers during winter months, it is quite conceivable that more pollen and more viable pollen will be produced, the stigmas will be more receptive, and the ovules more viable when the photosynthetic processes of the plant permit a higher degree of maturity of these organs during longer days. The capsules will ripen more quickly during the long summer days. It is also possible that some varieties that do not develop anthers, or which form only rudimentary anthers, during the winter, may produce pollen in the summer. This would permit selfing of these varieties.

The frequent appearance of abnormal types, many of which are lethal, has been a source of disappointment to a number of breeders. However, there are some varieties that show considerable virility in F_1 and F_2 progeny. It would seem logical to use these varieties to study inheritance in

the carnation, and in developing new commercial varieties.

It would be a great advance to have, on the commercial market, varieties of proven resistance to rust and stem rot, and these diseases require attention in a breeding program.

Doubleness in the carnation is mainly brought about by:

(a) Multiplication of the petals by division;

(b) Multiplication of the stamens with subsequent petalody of all or part of them.

The results from the crosses show that doubleness is more complex than has been previously believed. The small populations used by the earlier workers led them to hastily formed conclusions. From the results of these crosses and a study of the morphology of the flower it becomes apparent that split calyces are usually caused by the presence of adventitious buds within the flower. These buds, although depending upon doubleness for expression, do not necessarily indicate homozygous doubleness. Furthermore, some unsplit doubles with no signs of adventitious buds approach a homozygous condition for doubleness.

The appearance of a larger number of styles in the presence of carpellous ovules is an interesting detail, although no commercial value can be seen from this information.

As previously mentioned, this study, besides consisting of an examination of breeding methods and an attempt to deter-

mine inheritance of some characters, was an effort to produce varieties superior to those presently grown commercially. From the many seedlings grown six have been selected which show great promise. It is now intended to propagate these in considerable numbers and distribute them among commercial growers for testing under commercial growing conditions against the leading varieties.

CONCLUSIONS

1. Carnation breeding should be done during the summer months, when the long days will ensure a high percentage of successful crosses. A higher number of seeds per cross can also be expected.

2. The prevalence of abnormal types in the progeny of many commercial varieties, makes a study of inheritance difficult.

3. Doubleness is not the expression of one dominant factor as previously assumed, ~~but is caused by two or more factors~~, ~~or is quantitative in nature~~.

4. The presence of carpellous ovules in the ovary is frequently accompanied by an increase in the number of styles arising from the apex of the ovary.

5. Adventitious buds within the flower are the main cause of split calyces.

6. Adventitious buds, although dependent upon doubleness for expression, do not necessarily indicate homozygous doubleness.

7. Six promising new seedlings, in a range of color, have been developed in the course of this work.

APPENDIX "A"

Code Number	Variety	Code Number	Variety
1	Betty Lou	34	4314-A
2	Bonanza	35	4321
3	Chief Kokomo	36	4325-A
4	Dandy	37	4325-C
5	Early Rose	38	4341-B
6	Eleanor	39	4343-A
7	Golden Wonder	40	4344-B
8	Harvester	41	4345-A
9	Johnson's Crimson	42	4345-B
10	King Cardinal	43	4347-B
11	Maine Sunshine	44	4350-C
12	Mina Brenner	45	4354-A
13	My Love	46	4363-B
14	Ocean Spray	47	4363-C
15	Olivette	48	4363-D
16	Orchid Beauty	49	4363-E
17	Patrician	50	4363-H
18	Pelargonium	51	4363-O
19	Peter Fisher	52	4374-D
20	Pharoah	53	4374-G
21	Pink Abundance	54	4394-B
22	Pink Sensation	55	43100-A
23	Potentate	56	43100-B
24	Red Laddie	57	43105-A
25	Rose Charm	58	4217-C split-double
26	Spectrum Supreme	59	4303-A single
27	Spicy White	60	4318-A single
28	Topsy	61	4325-E split-double
29	Virginia	62	4325-F split-double
30	White Matchless	63	4344-C single
31	White Variegated	64	4357-F single
32	4001	65	4366-F single
33	4308	66	4369-A split-double

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